Plant and Soil (2005) 270: 321–330
DOI 10.1007/s11104-004-1726-x

Light and tree size influence belowground development in yellow birch and sugar maple

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Received 6 April 2004. Accepted in revised form 2 August 2004

Key words: light, mycorrhizal colonization, roots, sugar maple, yellow birch

Abstract

The effects of light and tree size on the root architecture and mycorrhiza of yellow birch (*Betula alleghaniensis* Britton) and sugar maple (*Acer saccharum* Marsh) growing in the understory of deciduous forests in southern Québec, Canada were studied. At the study site, small (<50 m^2), medium (101–200 m^2) and large (201–500 m^2) canopy gaps were investigated. From within these gaps, 17 yellow birch and 23 sugar maple saplings from 40 to 600 cm in height were sampled. In both species, root biomass and morphological traits were strongly correlated with tree size, but only weakly with light availability. Increased root biomass was primarily allocated to coarse roots and secondarily to fine roots. Yellow birch roots were longer, had a larger area, more endings and branches and grew more rapidly than sugar maple roots. Mycorrhizal colonization increased with available light and declined with tree age in sugar maple and was positively associated with tree size in yellow birch. The study demonstrates that tree size is a very important determinant of how belowground systems acclimate to understory conditions.

Introduction

In most forests, about 70% of the sunlight is absorbed in the upper canopy layers and only 3–10% reaches the forest floor (Tang, 1997). Few *in situ* studies have reported the effects of this light gradient on either the roots or, especially, the mycorrhiza of young trees. The availability of light is, however, known to influence the belowground growth of understory saplings (Leverenz, 1996). Fitter et al. (1998) reported that light controls the growth of plant roots in grassland and that optimum root growth occurs at 45–50% of full sunlight. Improved light increases root biomass (Fitter et al., 1998) and new root length (Noland et al., 1997) but decreases the root biomass ratio (defined as total root biomass/total plant biomass) (Walters and Reich, 1996, 2000).

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A typical tree root system consists of roots of various diameters. Generally, the smaller roots have more tips and branches than the larger roots. The proportion of vascular and cortical tissues in roots decreases as the diameter decreases (McCully, 1990). The changes in root architecture and anatomy associated with root development determine the ability of the roots to take up soil water and nutrients (McCully, 1990; Kolek and Kozinika, 1992). The aboveground tree size positively affects root development, sequentially increasing root diameters and modifying root metabolism and function (Kolek and Kozinika, 1992). How increased root biomass is allocated to the various sized roots of the taproot system of a tree and how it affects the morphological traits in different sized root systems is, however, unknown.

Generally trees grow bigger with age. However, in some stressful environments, such as a very shaded understory, the tree size (height) is only weakly correlated with age. Recent studies have been concerned

with the effects of tree size on changes in various tree traits. Messier and Nikinmmaa (2000) and Claveau et al. (2002) have shown that an increase in tree size leads to important changes in numerous traits, which in turn affect growth and survival. For example, height growth cooperates with canopy development in order to increase light capture. Tree size, therefore, has direct effects on the aboveground physiological and morphological traits of the tree (Walters et al., 1993; Lieffers et al., 1996; Claveau et al., 2002). However, how tree size influences root biomass allocation, morphological traits and the development of mycorrhiza remains unknown.

Both yellow birch and sugar maple seedlings colonize gaps in the mixed forests of southern Québec, Canada. Yellow birch is an ectomycorrhizal (ECM) species that is more moderately shade-tolerant than the arbuscular mycorrhizal (AM) species, sugar maple. Generally, mycorrhizal colonization, mycelium and spore production in the soil are positively correlated with light (Bethlenfalvay and Pacovsky, 1983). Increased light availability causes more photosynthate to be allocated to the roots (Fitter et al., 1998) for mycorrhizal formation. How this increased total root biomass affects mycorrhizal colonization is also unclear. As they age, some crop plants respond negatively to the AM association, as the resistance of roots to fungi may increase with age (Hayman, 1974; Franken and Gnädinger, 1994). There is, however, no information concerning this latter effect in trees.

This study, therefore, was undertaken to examine the responses of roots and mycorrhiza to changes in tree size and light created by selective cutting methods in naturally established saplings of both yellow birch and sugar maple. The study attempted to test the hypotheses that: (1) both light and tree size affect root biomass allocation, root morphology and mycorrhizal colonization; (2) the ECM moderately-shade tolerant yellow birch is more affected by both light and tree size gradients than the AM, shade tolerant sugar maple.

Materials and methods

Study site

The study was conducted in the Duchesnay Experimental Forest Station 46°55′ N, 71°40′ W, near Québec City, Canada, located on a moderate slope at an elevation between 200 and 300 m. The soil is a moder with a humo-ferric podzol underlain by well-drained glacial till. The mean annual precipitation is 1200 mm and the mean daily temperature ranges from −13 to 28 °C from January to July (Environment Canada, 1982). In the stands, the overstory is dominated by sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton) (60, 20 and 15% of merchantable volume, respectively) (Majcen and Richard, 1993). American yew (*Taxus canadensis* Marsh), mooseberry (*Viburnum alnifolium* Marsh), and striped maple (*Acer pensylvanicum* L.) grow in the understory. Pin cherry (*Prunus pensylvanica* L. f.), red-berried elder (*Sambucus pubens* Michx.) and raspberry (*Rubus idaeus* L.) are sometimes found in canopy gaps.

Experimental design

The experiment was established in 1995. Selective cuts that were made in 1988–89, 1993–94 and 1994–95 were selected to provide us with a gradient of gap sizes (ranging from <50 to 500 m^2), sapling sizes and ages. The gaps were classified as either small (<50 m^2), medium (101–200 m^2) or large (201–500 m^2). A series of between 20 and 35 gaps for each gap size were investigated throughout the study for 4 full growing seasons. Within these gaps, 17 yellow birch and 23 sugar maple saplings were randomly selected for harvesting out of a population of around 600 individuals that were previously marked. The saplings that were sampled were scattered among the different gap sizes to provide a range of light regimes.

Light measurements

The light available to the saplings was measured during 4 homogenously overcast days during the month of July 2000, using the method of Messier and Puttonen (1995); three instantaneous light measurements were taken 5 cm above the top of the saplings using a LI-189 light radiometer (LI-COR, Lincoln, Nebraska, USA). At the same time, a quantum sensor linked to a LI-1000 datalogger (LI-COR, Lincoln, Nebraska, USA) recorded light every minute in an adjacent open area. To calculate the percentage of total overstory PPFD (photosynthetic photon flux density) available, the values from above the trees were divided by the reference value taken at the same time in the open area. These punctual light measurements have been shown to be highly correlated with the mean seasonal daily percent PPFD as measured under overcast and clear sky (Gendron et al., 1998).

Root sampling

The entire root system of each selected tree was very carefully excavated by hand to avoid disrupting the finest roots. We collected as much fine root biomass for each tree as possible by cautiously digging out each root by hand. To do so, a team of 4 to 6 persons took up to 40 h to dig out the root system of one large 4 m tall sapling. Before each root system was fully harvested, 4 to 6 sub-samples of at least 20 cm length were removed and placed in a Ziploc bag then in a cooler with ice, to minimize water loss and root respiration. The whole root systems, plus the sub-samples, used for mycorrhizal and morphological measurements of the small fine roots (≤ 2 mm in diameter), were delivered to the field lab. The roots and sub-samples were washed free of soil, using a hose and the roots were retained for further analyses. Small roots were supported on a 32 mesh sieve during washing. Mycorrhizal samples were taken randomly from the sub-samples of each root system and the fresh weight was measured. The biomass of these sub-sub-samples was calculated from the ratio of the fresh weight of the other sub-sample to its dry weight.

Parameters investigated

The root system was divided into five diameter classes: 0.0–0.5, $>$0.5–1.0, $>$1.0–2.0 (subclasses of small fine roots), $>$2.0–5.0 (coarse fine roots) and $>$5 mm (coarse roots). For each diameter class, the following parameters were measured: (1) surface area (dm^2), (2) length (m), (3) number of forks, (4) number of endings (for fine roots, the endings were root tips, whereas for coarse roots, the endings were partially small fibrous roots), and (5) volume (mm^3). To describe the root morphology, the following ratios for each size class were calculated: area/biomass ($dm^2\ g^{-1}$), length/biomass (m g^{-1})(specific root length), endings/biomass (no. g^{-1}) and branches/biomass (no. g^{-1}). Root branches were calculated as forks/biomass (no. g^{-1}). Total root biomass (including sub-samples and sub-sub-samples), tree height (m) and tree age (year) were also recorded. The mycorrhizal colonization (percentage of root tips colonized for the ECM of yellow birch and percentages of intramatrical hyphae, coils, vesicles and arbuscules as well as total colonization for the AM of sugar maple) was also assessed.

Measurements

Measurements for the small fine roots were made within three hours of excavation so that shrinkage due to water loss was minimized. A McRhizo system (Regent Instruments Inc., Québec City, Québec, Canada) was used to scan the fresh sub-samples from each tree and to measure the surface area, volume, length and numbers of endings, separately, for the 0.0–0.5 mm, $>$0.5–1.0 mm and $>$1.0–2.0 mm root diameter classes and the total number of forks in each class. After fully harvesting the whole root system of each tree, the roots were sorted into small fine roots, coarse fine roots and coarse roots within five hours, using a digital caliper. Five fresh samples of the mid-diameter roots in each size category were selected to measure the morphological parameters using the McRhizo system. The total biomass of each of the three diameter classes was measured using a digital balance after drying in an oven at 70 °C for 48 h. Each of the parameters (P) (root surface area or length or endings) in the three classes was calculated as:

$$P = \left(\frac{TDW}{SDW}\right) \times VSP,$$

where *TDW* is the total dry weight in that diameter class; *SDW* is the dry weight of the dry samples in the same class; *VSP* is the value of the parameter in the dry samples. For the 0.0–0.5, $>$0.5–1.0 and $>$1.0–2.0 mm diameter classes, root surface area, length and endings were calculated using the percentages obtained from the fresh sub-samples. The root forks and biomass for the 3 small fine root diameter classes were calculated separately as:

$$F = \left(\frac{SRV}{TRV}\right) \times TRF,$$

where F is the fork number or the biomass for each of the small fine root classes; *SRV* is the root volume of the fresh sub-sample in the same class of small fine roots; *TRV* is the total root volume of the fresh sample in the ≤ 2 mm diameter classes; *TRF* is the total number of root forks or the biomass for each of the three small fine root classes, as volume has a strongly linear relationship with biomass (Ozier-Lafontaine et al., 1999). To estimate the age of the tree, the rings on the basal disk of each tree were counted using a microscope.

Arbuscular mycorrhizal colonization

The samples from sugar maples for mycorrhizal analyses were fixed in FAA (formalin 50 mL, acetic acid

50 mL and 900 mL of 50% ethanol) for at least 24 h. The roots were autoclaved for 60 min in 10% KOH at 15 psi to remove the phenolics, rinsed with water, placed in 35% Hydrogen Peroxide (H_2O_2) for 1 h, rinsed in water and acidified in 15% HCl for 15 min. They were then stained in a solution of 85% lactic acid, 99.5% glycerin and Chlorazol Black E (4:4:1 v:v:v) at 90 °C for 45 min. After de-staining in a solution of 99.5% glycerol and 85% lactic acid (1:1 v:v), the roots were mounted on slides and squashed with a cover slip. The AM structures were examined using a Nikon Optiphot Differential Interference Contrast (DIC) Microscope at a magnification of either 200× or 400×. The AM colonization for each root sample was obtained using the magnified grid intersect method (McGonigle et al., 1990). One hundred intersects were evaluated for each sample, and the presence or absence of intramatrical hyphae, arbuscules, vesicles and coils was noted at each. The colonization level for each fungal structure was determined as the percentage of intersects for which it was present. Total colonization levels were obtained by counting all intersects that had at least one of the structures present.

Ectomycorrhizal colonization

The grid line intersect method (Goodman and Trofymow, 1998) was used to measure the frequency of ECM in yellow birch. Roots were cut into pieces of ∼0.5–1.0 cm and laid out in an INTEGRID™ Petri Dish (Becton Dickson Labware, Lincoln Park, NJ). The quantification of the ECM colonization was performed using a dissecting microscope. The mycorrhizal colonization from 50 to 100 pieces of each tree was recorded as the % of the total number of root tips colonized by ECM fungi.

Data analyses

Analysis of covariance (ANCOVA) (Fu, 1979; Huitema, 1980) was used to investigate the effects of species, available light, total root biomass (as a measure of tree size) and their interactions on the architectural properties and mycorrhizal colonization of the roots. In the analysis, available light and total root biomass were used as covariates, as both have been shown to have a significant effect on many traits of a tree (Messier and Nikinmmaa, 2000; Claveau et al., 2002). Regression analyses were used to examine the relationships between dependent and independent variables. Multiple regressions using forward stepwise analyses were used to examine the relationships between total root biomass and mycorrhizal colonization and light, tree height and tree age, respectively. All variables were graphically examined for the normality of their distribution, using histograms, and for homogeneity of variance using scatter plots. If necessary, variables were transformed logarithmically. After transformation, all the data were tested and satisfied the assumptions for ANCOVA and regression analyses. SPSS (version 10) statistical software (SPSS Inc. Chicago, USA) was used to perform the analyses.

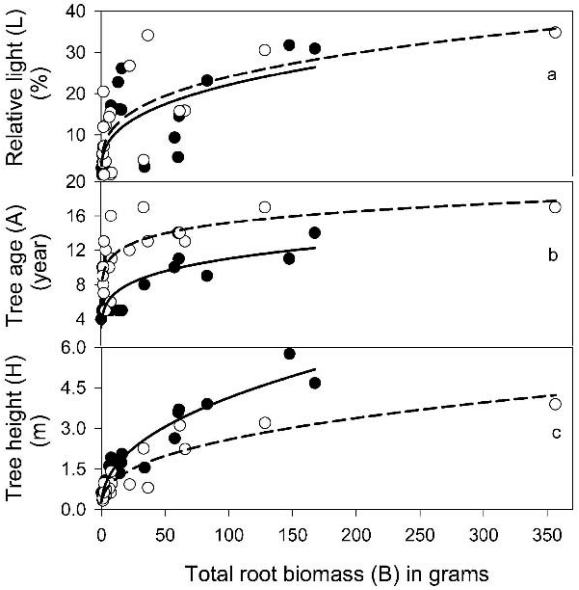

Figure 1. The relationships between total root biomass B (g), relative light L (%), tree age A(years) and height H (m) in yellow birch (YB = •, solid line) and sugar maple (SM = ○, dashed line. The regressions were, for light, $L_{YB} = 4.494B^{0.346}$, $R^2 = 0.44$ ($P < 0.00$); $L_{SM} = 5.747B^{0.311}$, $R^2 = 0.50$ ($P < 0.00$), for tree age, $A_{YB} = 4.270B^{0.206}$, $R^2 = 0.58$ ($P < 0.00$); $A_{SM} = 8.628B^{0.123}$, $R^2 = 0.52$ ($P < 0.00$), for tree height, $H_{YB} = 0.556B^{0.436}$, $R^2 = 0.90$ ($P < 0.00$); $H_{SM} = 0.434B^{0.367}$, $R^2 = 0.86$ ($P < 0.00$). The number of YB and SM sampled were 17 and 21, respectively.

Results

Effects of light, tree height and age on root biomass

In both species, total root biomass increased in a nonlinear manner as light, tree age and height increased (Figure 1). Stepwise linear regression analysis indicated that for both species tree height was the most important predictor of total root biomass, that age was not a significant predictor and that light was not a significant predictor for yellow birch and only a

Table 1. Stepwise (forward) linear regression analyses for the effects of light, tree age and height on total root biomass of yellow birch (YB) and sugar maple (SM) grown without shading cloths

Dependent variable	Independent variable	R^2
Total root biomass (YB)	$= -30.773 + 31.235$ (Height)	0.86
(Probability)	(0.000)	(0.000)
Total root biomass (YB)	$= -26.863 + 0.238$ (Height) $+0.425$ (Light) $+1.117$ (Age)	0.89
(Probability)		(0.000)
Total root biomass (SM)	$= -52.282 + 49.940$ (Height) $+2.193$ (Light)	0.73
(Probability)	(0.000) (0.044)	(0.000)
Total root biomass (SM)	$= -37.494 + 0.411$ (Height) $+2.225$ (Light) $+0.022$ (Age)	0.74
(Probability		(0.000)

marginally significant ($P = 0.044$) predictor of root biomass for sugar maple (Table 1). For a given height, yellow birch had less root biomass than sugar maples (Figure 1c).

Biomass allocation within the root system

In root systems up to a total biomass of $\sim$60 g, the proportion of coarse root biomass increased with increasing total root biomass for both species, while that of small fine roots decreased (Figure 2). Once root biomass exceeded 60 g, the proportions of coarse roots, small and coarse fine roots tended to remain constant as total root biomass increased in yellow birch, whereas, in sugar maple, the proportion of coarse roots was still gradually increasing (Figure 2).

Effects of total root biomass, light and species on root morphology

Both tree species and total root biomass (tree size) had a significant or marginally significant effect on many morphological traits of the root, whereas light generally did not (Table 2). The significant interaction of species $\times$ tree size (root biomass) for the root area/biomass ratios and the effect of total root biomass on branches/biomass ratios indicated that, for both species, these ratios declined with increasing root biomass, but the effect on the root area over biomass ratio was different between the two species and was not significant for yellow birch (Figure 3).

The specific root length and the ratios of root surface area, endings and branches to root biomass for many root diameter classes of yellow birch were generally higher than those of sugar maple (Figure 4). The largest difference between the two species was found in the ratio of the numbers of endings/biomass (Figure 4c). This ratio was the highest for the small fine roots up to 1.0 mm, and then declined for the coarse fine roots and the coarse roots (Figure 4c). Generally, these ratios were much smaller for the larger size classes (>2–5 mm) of roots (Figure 4).

Mycorrhizal colonization in relation to light, tree size and age

Stepwise regression analysis of the relationship between light, tree age, height, and mycorrhizal colonization showed that tree height had a small, significant, positive effect on mycorrhizal colonization in yellow birch ($R^2 = 0.26$, $P = 0.04$; data not shown). In sugar maple, light had a significant positive effect and age a negative effect on total colonization (AM colonization $= 78.617 + 1.049$ (Light ($P < 0.000$)) – 2.343 (Age ($P = 0.003$) ($R^2 = 0.06$; $P < 0.00$; data not shown).

Discussion

Effects of light and tree size on root traits

In both yellow birch and sugar maple, total root biomass was found to be the major determinant of root traits (Table 2). Root biomass was positively related to tree height, and, to a lesser extent, to light availability (Table 1). Tree size aboveground (height) affects the ability of the tree to survive in low light (Messier et al., 1999), as the size determines changes in many aboveground traits of the tree (Walters et al., 1993; Lieffers et al., 1996; Claveau et al., 2002; Delagrange et al., 2004) which enable it to capture more light (Claveau

Table 2. Analysis of covariance of the effects of tree species on the specific root length (m g^{-1}), surface area/biomass (dm^2 g^{-1}), endings/biomass (no. g^{-1}) and branches/biomass (no. g^{-1}) ratios in the five root classes. Light (0.3–35% of full sunlight) and total root biomass are the covariates. F is the mean square ratio. * significant at $P < 0.05$. ** significant at $P < 0.01$. Bolded numbers indicate a significant difference. Data for non-significant interactions are not shown

Source	Root diameter class (mm)	Area/Biomass F	Specific root length	Endings/Biomass F	Branches/Biomass F
Species (S)	0.0–0.5	2.084	0.045	**18.43****	0.435
	>0.5–1.0	3.609	0.180	**22.84****	0.947
	>1.0–2.0	**4.319***	0.218	**25.15****	**6.138***
	>2.0–5.0	**4.592***	0.053	**8.402****	0.518
	>5.0	**15.98****	**14.81****	0.253	**5.343***
Light (L)	0.0–0.5	0.708	0.155	0.928	2.224
	>0.5–1.0	0.674	0.184	1.430	0.838
	>1.0–2.0	0.193	0.159	**7.878***	0.000
	>2.0–5.0	0.548	0.001	0.034	0.696
	>5.0	0.760	3.032	0.073	3.749
Total root biomass (B)	0.0–0.5	**5.380***	0.398	0.080	**46.99****
	>0.5–1.0	**8.435****	0.937	0.029	**62.82****
	>1.0–2.0	**6.649***	1.010	**6.426***	**181.6****
	>2.0–5.0	**6.406***	1.173	4.113	**63.89****
	>5.0	**15.49****	3.686	0.611	**19.79****
S × B	0.0–0.5	3.724	0.821	0.972	0.044
	>0.5–1.0	**5.254***	1.301	2.162	0.168
	>1.0–2.0	**5.472***	1.387	0.002	0.058
	>2.0–5.0	**5.676***	0.518	1.791	2.118
	>5.0	**12.54****	1.186	1.978	4.374

et al., 2002) and, indirectly, affects nutrient acquisition by its association with total root biomass. As the root develops, the main function of the accumulating biomass changes from traits associated with soil exploration and nutrient acquisition to building structural tissues for support and storage.

Light was not found to directly affect root morphology (Table 2). Although Noland et al. (1997) reported that light increases root length in jack pine seedlings, our data show that the specific root lengths of the various size classes of roots do not respond directly to light (Table 2), but that the increase in root length is directly proportional to the increase in root biomass as light increases. As reported elsewhere, it is possible that the reported relationship between light and many root traits is only indirect, as trees receiving more light are usually larger (Claveau et al., 2002; Delagrange et al., 2004). Thus, light probably affects root architecture only indirectly through its effects on tree size. As the tree size increases, more carbohydrates are assimilated and more reserves are available to the tree, resulting in increased carbohydrate transport to the root system (Ericsson et al., 1996). Light may also indirectly increase root biomass by increasing soil temperature, moisture and nutrients (Zak et al., 1993), by stimulating microbial activities (Nakazato et al., 1999) and by enhancing mycorrhizal colonization (Parke et al., 1984; Parsons et al., 1994, this study). However, DeBellis (2000) found no significant differences in the soil temperature, water, pH and nutrients under the different sized canopy gaps in an adjacent forest.

Biomass allocation within the root system

As total root biomass increases, the proportion allocated to fine roots progressively decreases whereas the proportion of biomass allocated to the coarse roots progressively increases. The absolute amount of small fine root biomass, however, increases continuously as the root system grows. This is very similar to the behavior of the leaf component aboveground,

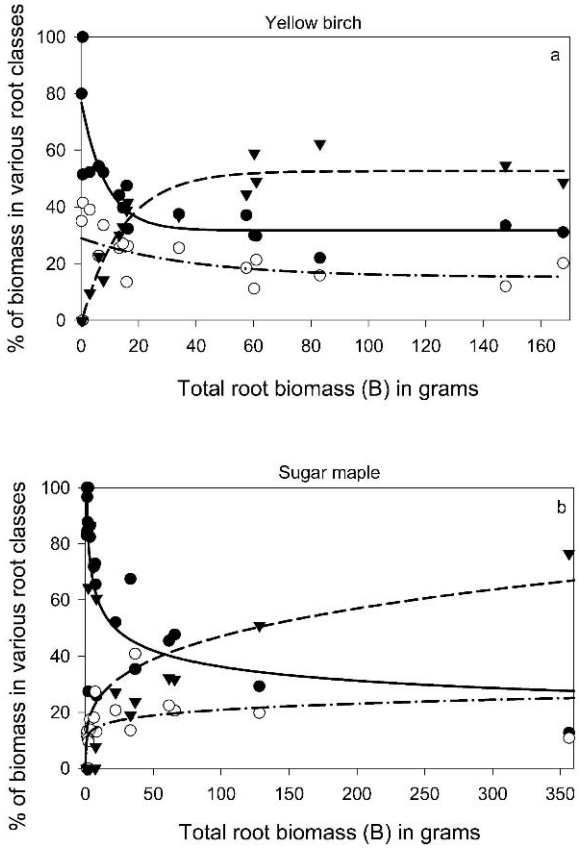

Figure 2. Changes in proportions (%) of coarse (> 5 mm) roots (▼, dashed line), coarse fine (> 2 mm, < 5 mm) roots (○, dashed and dotted line) and small fine (< 2 mm) roots (●, solid line), as a percentage of biomass of yellow birch and sugar maple with increasing total biomass in grams (B) of the roots. The regressions were, for yellow birch, coarse roots (C), $C = 52.670 - 54.04\ e^{-0.070B}$, $R^2 = 0.93$ ($P < 0.00$); coarse fine roots (M), $M = 15.250 + 13.740e^{-0.026B}$, $R^2 = 0.21$ ($P = 0.04$); small fine roots (S), $S = 31.690 + 46.460\ e^{-0.118B}$, $R^2 = 0.74$ ($P < 0.00$) and for sugar maple, $C = 13.250B^{0.275}$, $R^2 = 0.23$ ($P = 0.03$); $M = 10.760B^{0.144}$, $R^2 = 0.20$ ($P = 0.04$); $S = 96.460B^{-0.213}$, $R^2 = 0.59$ ($P < 0.00$).

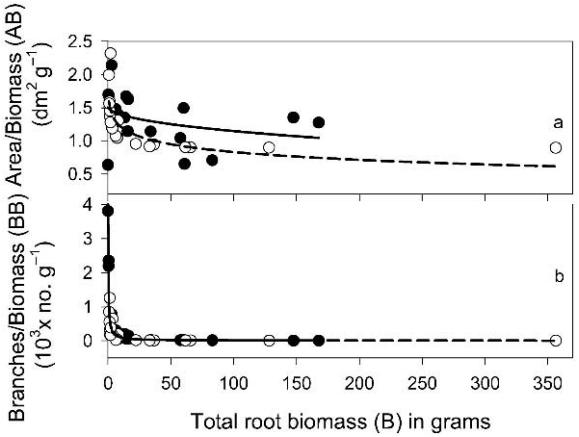

Figure 3. Effects of species and total root biomass (g) on the root surface area/biomass ($dm^2\ g^{-1}$) and branches/biomass (no. g^{-1}) ratios of <1.0–2.0 mm diameter root class in yellow birch (YB = ●, solid line) and sugar maple (SM = ○, dashed line). The regressions were, for the Area/Biomass ratios, (AB), $AB_{YB} = 1.528 - 0.046B^{0.460}$, $R^2 = 0.12$ ($P = 0.15$); $AB_{SM} = 31.640 - 30.040B^{0.005}$, $R^2 = 0.56$ ($P < 0.00$) and for the Branches to Biomass ratios (BB), $BB_{YB} = 1/(B + 0.049)$, $R^2 = 0.91$ ($P < 0.00$); $BB_{SM} = 1/(B + 0.291)$, $R^2 = 0.56$ ($P < 0.00$). These ratios showed similar patterns in the other diameter classes.

which continuously increases with tree size, but to a lesser extent than the branches and the trunk (Messier and Nikinmaa, 2000; Delagrange et al., 2004). The rapidly developing coarse roots establish a strong root skeleton and physically support and anchor the aboveground growth of the tree. However, in coarse roots, the epidermis has been modified to become impermeable (McCully, 1990). Coarse roots, therefore, lose almost all of their absorptive ability and function mainly as storage organs for starch for future growth of the tree.

Our data emphasize that it is the small fine roots that have the largest numbers of tips and branches (Figure 4) and explore the largest volume of soil in relation to the coarse roots. The living endings (tips) of fine roots are permeable to soil water and mineral nutrients (McCully, 1990), and thus, it is these that play the major role in water and nutrient uptake, most of which occurs in the first 4–5 cm of the roots (Kolek and Kozinika, 1992). Thus, biomass allocated to the coarse roots contributes to structure and storage, while that allocated to fine roots contributes to nutrient and water acquisition.

The biomass allocated to the various size classes of roots become more or less constant after the root systems of the yellow birch reached a total biomass of ~60 g (Figure 2). The change in investment of root biomass to various root size classes and structures may balance the requirements for aboveground and belowground growth of the tree. We observed change in the efficiency of small fine roots to expand its root area between species as total root biomass increases (Figure 3a). In very young sugar maples, the root area over biomass ratio is higher than yellow birch, but rapidly as total root biomass increases sugar maple has a lower ratio. One possible reason for the decline in root area over biomass with increasing total root biomass is that more carbohydrates are used by the fine roots to increase root respiration (Roberts et al., 1993) to support water and nutrient uptake and transport, and to

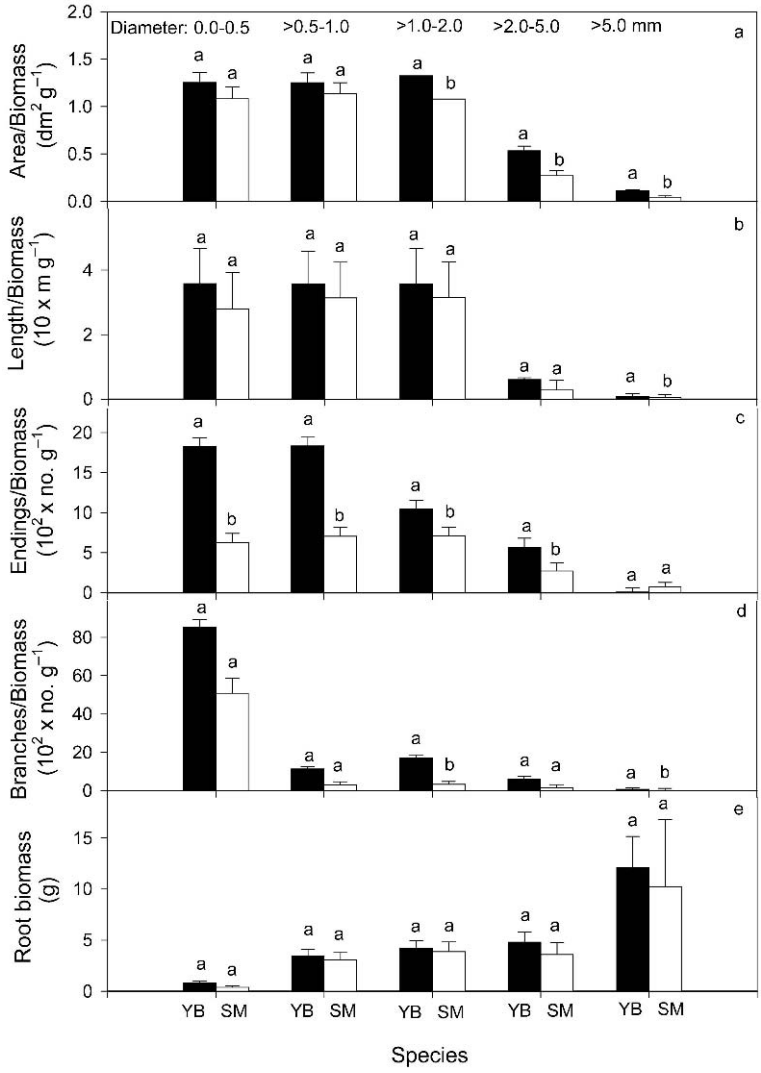

Figure 4. Root surface area/biomass (dm^2 g^{-1}) length/biomass (m g^{-1}), endings/biomass (no. g^{-1}), branches/biomass (no. g^{-1}) ratios and root biomass (g) in different sized roots of yellow birch (YB = ■) and sugar maple (SM = □). Error bars represent the standard error (SE) of the mean. Means with the same letter do not differ significantly from each other ($P > 0.05$).

increase the formation of symbiotic associations and exudations that support microbial activities in the soil (Lambers, 1990).

Roots of yellow birch grow more rapidly than those of sugar maple. The average age for both species was similar, around 9 years old for yellow birch and 11.5 years old for sugar maple. For total root biomass, Figure 1b indicates that, for a given age, the total biomass of yellow birch roots is greater than that of sugar maple roots. Architecturally, yellow birch generally tends to have a greater root area, length and more endings and branches per unit of root biomass than sugar maple (Figure 4), suggesting that the roots of yellow birch develop faster and occupy more soil volume than do those of sugar maple. Compared to sugar maple, yellow birch is a moderately shade-tolerant species and has higher photosynthetic, transpiration and respiration rates (Walters and Reich, 2000; Delagrange et al., 2004). Therefore, to satisfy its physiological needs, yellow birch in the understory needs to take up more water and nutrients from the soil by the rapid development of the root system.

Mycorrhizal colonization

Different types of mycorrhiza have different responses to a changing environment, since biotic factors may interactively affect mycorrhizal development. The % of the root system colonized by ectomycorrhizal fungi (yellow birch) or % arbuscular mycorrhizal colonization of sugar maple increases as tree size or light increases. However, the ectomycorrhizal colonization of yellow birch appears mainly to respond to size, not to the light gradient. High light availability results in rapid height growth in yellow birch. The increased height coincidently promotes the crown development for more production of photosynthates which will promote ectomycorrhizal development. For understory sugar maple, the light gradient affects the arbuscular mycorrhizal colonization, but the coefficients of determination are low. The different responses of mycorrhizal colonization to changing light in both species suggest that the effect of light on mycorrhizal development is indirect. Increased light generally increases leaf carbohydrate levels, such as starch and sugars. This results in higher translocation to the roots (Corre, 1983; Hodge et al., 1997), sequentially enhancing the exudation of sugars, amino acids, amides and phenolic acids to the soil (Grayston et al., 1996). This promotes the development of mycorrhizal and rhizosphere associations. In the arbuscular mycorrhizae of sugar maple, the intramatrical hyphae increased with light whereas the arbuscules and coils do not.

The absolute amount of mycorrhizae is positively correlated with increased root biomass in both species. Our study indicates that total root biomass has no effect on ectomycorrhizal or arbuscular mycorrhizal colonization rates and no significant relationship between the rates of colonization and the biomass of the small fine roots of either species are found. Increased total root biomass increases the absolute amount of small fine root biomass, leading to increases in the surface area, length, endings and branches of the small fine roots. Although the mycorrhizal colonization rates do not change, the total amount of mycorrhizal fungus in the root systems of both species must increase as total root biomass increases. The total number of mycorrhizae in a root system will, therefore, have a positive relationship with the total root biomass.

Tree age affects the arbuscular mycorrhizal colonization of sugar maple roots only. However, mycorrhizal fungi are normally only associated with the very fine roots of trees, which generally have a very high annual turnover rate. Thus, tree age will influence total ectomycorrhizae in yellow birch and total arbuscular mycorrhizae in sugar maple because older trees with larger root systems will have relatively fewer fine roots available for colonization.

Conclusions

The ability of understory tree saplings to modify their belowground allocation, root traits and mycorrhizae is greatly influenced by tree size and much less by light. These findings agree with recent similar conclusions reported in the literature for aboveground traits. In this context, many previous studies that associated changes in belowground allocation, root traits and mycorrhizae to light may need to be reevaluated. We also have shown that root surface area, length, endings and branches are mainly formed in the small fine roots, where maximal respiration, water and nutrient transport (McCully, 1990; Pergitzer et al., 1997) occur. As these are critical functions for the survival of saplings, more research attention should be focused on the small fine roots.

Acknowledgements

This study was supported by Concordia University Graduate Fellowship to S. Cheng and by an NSERC strategic grant to the junior author C. Messier (PI). The authors are also grateful to Joel Coburn, Sylvain Delagrange, Marie-Hélène Croisetière, Julie M. Richard, Nathalie Bourdonnais-Spear, Jocelyn Poissant, Mario Bonneau, Alexandre Piboule, Johanne Campbell and Rebecca Tittler for assistance in the field.

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Section editor: J.W.G. Cairney